

A test of functional convergence in carbon fluxes from coupled C and N cycles in Arctic tundra

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ABSTRACT

Arctic ecosystems exhibit functional convergence in Net Ecosystem Exchange (NEE's) of CO₂ response to light, air temperature, the Normalized Difference Vegetation Index (NDVI), and Leaf Area Index (LAI), potentially simplifying predictions of climate change impacts on the arctic C cycle over space and time. This convergence is hypothesized to be induced by tightly coupled carbon and nitrogen cycles, but has never been explicitly tested. We used model-data fusion on a mass balance model (i.e. the Coupled Carbon and Nitrogen; CCaN) to determine whether functional convergence in NEE results from tightly coupled carbon (C) and nitrogen (N) cycles. CCaN captured a majority, but not all, of NEE and NDVI observations across eight growing seasons, and MODIS NDVI observations across a tundra latitudinal gradient in Alaska. The hypothesis of temporal functional convergence was challenged by model-data disagreements for NEE during shoulder seasons and low light. The hypothesis of spatial functional convergence was challenged by the underestimation of NDVI in warm tundra. CCaN structure and parameter uncertainty analyses revealed that factors controlling leaf litter rate, the proportion of N in leaves, and net N mineralization rate are critical knowledge gaps in predicting pan-arctic NEE and NDVI in a future warmer climate.

1. Introduction

Arctic tundra ecosystems illustrate surprising convergence in the net uptake of CO₂ from the atmosphere (i.e. the Net Ecosystem Exchange of CO₂ (NEE)), despite large variability in soils climate, and vegetation cover (Shaver et al., 2007, 2013). This functional convergence is demonstrated by the ability to accurately model the spatial and temporal dynamics in the Net Ecosystem Exchange of CO₂ with a single functional response to light, temperature, and the Normalized Difference Vegetation Index—a spectral reflectance based proxy of Leaf Area Index (LAI) (Shaver et al., 2007; Loranty et al., 2011; Shaver et al., 2013). Understanding functional convergence is important because it can simplify C cycling predictions in a rapidly changing environment and help determine whether increased temperatures will make the arctic a future C source or sink. A limitation of the functional convergence model, however, is that it requires LAI to predict NEE, which is often difficult to predict in ecosystem models. Hence, a mechanistic understanding of C uptake and allocation to LAI is needed to predict future carbon cycling with the functional convergence model.

In arctic ecosystems, a simple and strong relationship exists between foliar N and canopy LAI across a wide variety of tundra communities (Fig. 1). This relationship arises as a unique emergent property at the

plant community level and reflects both the strong N limitation in arctic systems and a stoichiometric N cost of producing canopy leaf area and increasing photosynthetic potential (Williams and Rastetter, 1999; van Wijk et al., 2005). This relationship is important because it may allow for the prediction of both LAI and NEE in the functional convergence model provided knowledge of N cycling. Arctic ecosystems are thought to have relatively closed N cycles, where N internally recycles among biomass, soil organic matter, and available N pools due to the low rates of deposition, runoff, and mineralization of N (Shaver et al., 1992; Williams and Rastetter, 1999; Pearce et al., 2015; Jiang et al., 2015). N can impose substantial biological constraints on soil and plant C cycling that may contribute to the observed functionally convergent responses of NEE to light, temperature, and LAI. Consequently, we hypothesize that coupled C and N cycling and functional convergence can be used to predict arctic NEE and NDVI.

Simple ecosystem models provide a means to further understand the dependence of functional convergence on tightly coupled tundra C and N cycles. Such models provide quantitative frameworks to corroborate or challenge our current understanding of ecosystems (Ågren and Bosatta, 1990; Rastetter, 2003; Rastetter et al., 2003; Dietze et al., 2013). Agreement between models and data indicate a parsimonious understanding of ecosystem function, while disagreement between

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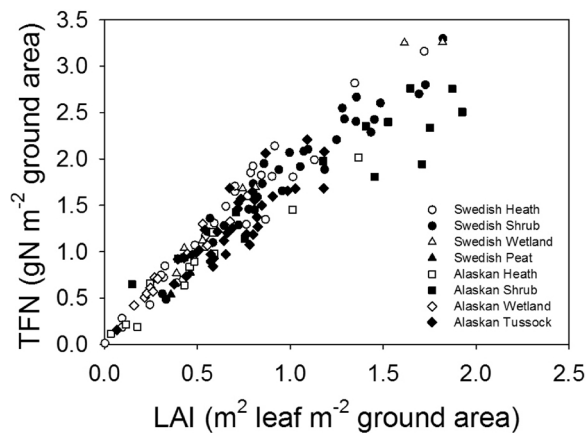


Fig. 1. Relationship between total foliar N (TFN) and the Leaf Area Index (LAI) of arctic ecosystems (Redrawn from Williams and Rastetter, 1999; van Wijk et al., 2005).

models and data highlights gaps in model structure and current understanding (Rastetter et al., 2003; Rastetter, 2017). Assessing model-data agreement is challenging however because uncertainty can be as large as the measurement itself, model parameters regulating ecosystem processes can be biologically unrealistic, and model parameters can offset one another through covariation, resulting in correct model predictions for the wrong reasons (Raupach et al., 2005; Luo et al., 2009; Keenan et al., 2011). One way to overcome these issues is to incorporate model and data uncertainty during parameterization through model-data fusion (Williams et al., 2005; Keenan et al., 2012; Dietze et al., 2013; LeBauer et al., 2013). Model-data fusion is an iterative technique used to find the best set of parameters that fit a proposed model to data with quantified uncertainties. Since model-data fusion statistically characterizes both model and data uncertainty and incorporates biological constraints into model parameterization, it provides a robust method to detect model-data disagreements.

We used model-data fusion with a simple mass balance model (i.e. the Coupled Carbon and Nitrogen model; CCaN) to test the hypothesis that coupled C and N cycling and functional convergence can be used to predict arctic NEE and NDVI. We developed CCaN instead of using other more commonly used C cycling models for several reasons. First, CCaN's simplicity allowed us to avoid issues of overfitting and equifinality that can limit process based understanding from more complex models. Second, CCaN's simplicity also allowed us to relate model processes to actual field measurements to constrain model parameters within realistic and biologically valid limits during CCaN model-data assimilation. Third, CCaN's simplicity allowed us to better diagnose processes that resulted in model-data disagreements with statistical certainty, and thus, highlight ecosystem process that require further understanding. Lastly, CCaN is the only model to link the tight relationship between foliar N and LAI in van Wijk et al., 2005 and Williams and Rastetter (1999) to the functional convergence in NEE as proposed by Shaver et al., 2007, 2013. Further understanding how the functional convergence of arctic CO₂ fluxes is related to tightly coupled C and N cycles will not only help to predict tundra C cycling, but also help constrain the responses of plants and soils to climate change.

2. Methods

2.1. Research Approach

We developed and parameterized a Coupled C and N mass balance model (CCaN) using model-data fusion with eddy covariance NEE and daily NDVI. Our approach followed the code of best practices for model-data fusion (Keenan et al., 2011) by: 1) quantifying measurement uncertainties, 2) testing our model-data fusion framework against

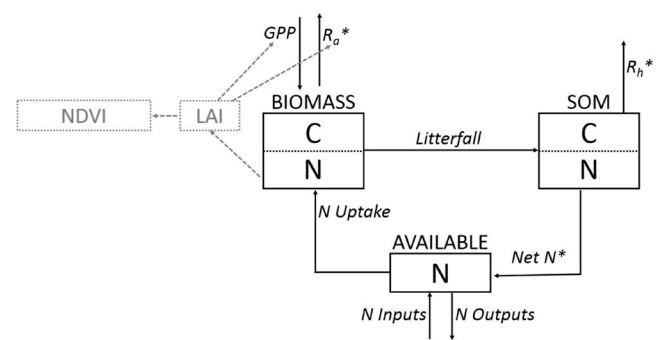


Fig. 2. CCaN model diagram. Boxes represent pools and solid arrows represent fluxes. Fluxes denoted with a “*” are temperature sensitive. Gray dashed boxes indicate other relevant model outputs, and the gray dashed arrows indicate their use in flux calculations.

synthetic data, 3) assimilating multiple data sources (i.e. NDVI and NEE) to estimate parameters, 4) testing model output with independent observations, 5) minimizing equifinality by choosing a simple model and carefully selecting free-parameters, and 6) incorporating quantified model and data uncertainties into model predictions. Our hypothesis was that coupled C and N cycling and functional convergence can be used to predict arctic NEE and NDVI. The test of this hypothesis is whether the CCaN model, using a single parameter set estimated with model-data fusion, can replicate the temporal and spatial dynamics of arctic NEE and NDVI provided both model and measurement uncertainty. The model and model-data fusion code were written in R and can be found on a GitHub page (https://github.com/kkremers/CCaN_MS2016.git).

2.2. CCaN Model

CCaN (Fig. 2) is a spin-off of the Simple Arctic Model (SAM, Shaver et al., 1992) in terms of its simplicity and N limitation on C fluxes. CCaN is consistent with the view of a relatively closed N cycle, where N is internally recycled among biomass, SOM, and available N pools (Shaver et al., 1992; Williams and Rastetter, 1999; Pearce et al., 2015; Jiang et al., 2015). CCaN was driven with daily light and air temperature and predicted daily NEE, LAI, and NDVI. CCaN equations and details can be found in the appendix and in Table 1, but we will briefly describe the model framework in the following section. CCaN pools are plant biomass C and N, soil organic matter (SOM) C and N, and available N (Table 1).

The functional convergence model for NEE controlled C moving into and out of the system. C inputs (GPP) were controlled by PAR and LAI. C is respired from biomass as autotrophic respiration (R_a), which is controlled by temperature and LAI, and from SOM pools as heterotrophic respiration (R_h), which is controlled by temperature alone. LAI is estimated by CCaN using a linear relationship with Total Foliar N (TFN) that is sensitive to biomass N, temperature, and vegetation phenology (Williams and Rastetter, 1999). LAI is converted to NDVI by inverting the exponential relationship derived from Shaver et al. (2007) and Rocha and Shaver, 2009 [Equation 3]. All parameters associated with the functional response of GPP, R_a , and R_h are derived from Loranty et al. (2011), which is a temporally scaled version of the original functional convergence model described in Shaver et al. (2007).

Along with the tight relationship between TFN and LAI, C and N cycles are coupled by several other processes in CCaN. Both biomass C and N moved to soil organic matter (SOM) through a shared litterfall rate. Plant uptake of N from the available N pool is limited by root biomass C and the amount of available N. Net N mineralization (Net N) transferred N from SOM to the available N pool, and is sensitive to temperature, the amount of SOM N, and a net mineralization rate. The available N pool also is influenced by smaller fluxes that included N

Table 1

Description of model parameters, pools, and fluxes. Parameters with a “*” were estimated with model-data fusion. Prior ranges are in parenthesis following parameter description.

Name	Description
<i>Parameters</i>	
K_{plant} (g N m^{-2}) *	Half saturation constant of nitrogen uptake (0.07, 0.34) ¹
LitterRate (day^{-1}) *	Rate of litter decomposition (0.0001, 0.0024) ²
UptakeRate (day^{-1}) *	Rate of nitrogen uptake (0.002, 0.012) ¹
propNfol ₀ (g N g^{-1} N biomass) *	Proportion of biomass N allocated to foliage when air temperature is 0 °C (0.01, 0.23) ³
propNroots (g N g^{-1} C biomass) *	Ratio of root N : biomass C (0.01, 0.022) ³
netNrate (day^{-1}) *	Net nitrogen mineralization rate (0.003, 0.04) ⁴
Q10 *	Q10 temperature coefficient of N mineralization (1, 3) ⁵
R_0 ($\text{g C m}^{-2} \text{ day}^{-1}$)	Basal respiration rate per unit leaf area (used in autotrophic respiration calculation) ⁶
beta ($^{\circ}\text{C}^{-1}$)	Temperature sensitivity of respiration ⁶
R_x ($\text{g C m}^{-2} \text{ day}^{-1}$)	Second basal respiration rate (used in heterotrophic respiration calculation) ⁶
P_{max} ($\text{g C m}^{-2} \text{ day}^{-1}$)	Maximum photosynthetic rate per unit of leaf area ⁶
E_0 (g C mol^{-1} photons)	Light use efficiency ⁶
<i>Pools</i> (g m^{-2})	
Biomass	C and N in plant biomass
SOM	C and N in soil organic matter
Available N	Inorganic nitrogen available for plant uptake
<i>Fluxes</i> ($\text{g m}^{-2} \text{ day}^{-1}$)	
GPP	Gross primary productivity - carbon uptake via photosynthesis
R_a	Autotrophic respiration - carbon release by plants
Litterfall	Transfer of plant biomass to SOM via litterfall and decomposition
R_h	Heterotrophic respiration - carbon release by heterotrophs
N outputs	Nitrogen leaching
N inputs	Deposition and fixation of atmospheric nitrogen
Net N	Net nitrogen mineralization by microbes
N uptake	Nitrogen uptake by plants

Superscripts for references are as follows: 1) Leadley et al. (1997), 2) Hobbie (1999), 3) Toolik LTER data (Gough et al., 2006), 4) Toolik LTER data (Demarco et al., 2006), 5) McLaughlin et al. (2014), and 6) Loranty et al. (2011).

deposition, fixation, and leaching, whose rates are obtained from LTER data (Shaver et al., 2014). Model-data fusion estimated CCaN parameters (K_{plant} , LitterRate, UptakeRate, propNfol₀, propNroots, netNrate, and Q10) associated with the N cycle, which were constrained by informed prior distributions from measurements, CCaN's coupled C and N cycles, and the observed relationship between TFN and LAI (Fig. 1; also see Table 1).

2.3. Available Datasets: Meteorological Measurements, Tower NDVI, and Uncertainty

Air temperature and PAR from the unburned Anaktuvuk River fire eddy covariance site during the 2008–2015 growing seasons (June–August) were used as environmental drivers for CCaN model parameterization and temporal corroboration. Details on instrumentation, site description, data processing, and quality control are described extensively elsewhere (Rocha and Shaver, 2009, 2011a; Rocha and Shaver, 2011b; Wang et al., 2012; Jiang et al., 2015). Briefly, the site was located in a homogenous ~5 km² patch of moist acidic tussock tundra approximately 40 km from the Toolik Lake LTER station (Rocha and Shaver, 2011a; Wang et al., 2012). Winter gaps in air temperature and PAR were filled with Toolik Field Station meteorological data located 40 km away. Daily average vapor pressure deficits (VPD) also were collected at the Anaktuvuk tower during the growing season. Daily precipitation data were collected by the Toolik LTER.

Half hourly reflected and incident PAR and shortwave radiation at

the Anaktuvuk tower were used to calculate daily averaged NDVI (Rocha and Shaver, 2009). Tower NDVI represented a broadband derivation of NDVI and needed to be converted to a narrowband NDVI to apply the appropriate NDVI-LAI relationship. This conversion was accomplished through a linear calibration between tower based NDVI and averaged NDVI spectroradiometer measurements ($n = 80$) taken within the footprint of the eddy covariance tower at bi-monthly intervals from 2008 to 2015 (see Supplementary Materials & Rocha and Shaver, 2009). NDVI uncertainty was estimated by comparing the scaled tower measurements to MODIS NDVI for the area encompassing the eddy covariance tower (see Supplementary Materials).

2.4. Available Datasets: Eddy Covariance Data, Gap Filling, and Uncertainty

Eddy covariance derived NEE from the unburned Anaktuvuk River site during the 2008–2015 growing seasons (June–August) were used to parameterize and corroborate CCaN. Half hourly NEE data were scaled to daily sums using quality control and gap filling techniques used by Ameriflux and Fluxnet (Reichstein et al., 2012). Data gaps were filled using a bulk NEE light and temperature response function that was parameterized every day using an 11 day window with least squares regression. NEE gaps comprised ~15% of the growing season measurement period with the longest gap lasting only a few days. Uncertainty in daily NEE was quantified using a paired tower approach that compared NEE from the unburned Anaktuvuk site to NEE from another site located less than 7 km away (see Supplementary Materials, Hollinger and Richardson, 2005; Richardson et al., 2008). NEE followed the meteorological sign convention with negative fluxes indicating CO₂ uptake, and positive fluxes indicating CO₂ loss from the land surface.

2.5. Available Datasets: Toolik LTER

Data on soils and vegetation from the Toolik LTER were used to assign biologically valid maximum and minimum parameter values during model-data fusion. Uniform prior distributions were established on all model parameters, which were bounded by maximum and minimum values obtained in the field (Table 1). Maximum and minimum net N mineralization (netNrate) rates were from a gradient of tundra community types within a snow fence experiment (Gough et al., 2006). Maximum and minimum proportion of biomass N in foliage (propNfol₀) and roots (propNroots) were obtained from undisturbed moist acidic tundra. Maximum and minimums for K_{plant} , LitterRate, UptakeRate, and Q10 were obtained from tussock tundra at or near Toolik Field station (Hobbie, 1999; Leadley et al., 1997; McLaughlin et al., 2014). The temperature sensitivity of the proportion of biomass N in foliage ($\bar{\alpha}$) was determined with the LTER greenhouse experimental plots, which warmed air temperatures by 5.6 °C (Shaver, 1998). $\bar{\alpha}$ was calculated as the biomass weighted average temperature sensitivity across the three most dominant vascular species (*Betula nana*, *Eriophorum vaginatum*, *Carex bigelowii*) in moist acidic tundra (Appendix Equation A17).

2.6. Available Datasets: MODIS and other Spatial Datasets

MODIS NDVI and surface temperature from 32 tundra sites along a North – South transect extending from 65 °N to 70 °N along Alaska's Dalton Highway were used to corroborate CCaN NDVI spatially. Three of the sites were located below 68 °N and were tundra situated in the boreal region, whereas the rest of the sites were situated North of Alaska's Brooks Range. This transect was chosen because it spanned a variety of tundra communities and soil conditions and because we have conducted detailed vegetation surveys at these sites. The transect includes all vegetation communities found on the North Slope of Alaska and ranged from erect-shrub tundra in the south, acidic and non-acidic graminoid tundra in the North Slope foothills, and wetland tundra in

the far north.

MODIS NDVI (MOD13Q1, 8-day, 250 m resolution) and night and day surface temperatures (MOD11A2, 8-day, 1 km resolution) were extracted for each site. MODIS quality control flags were used to remove low quality data. CCaN was driven with daily interpolated PAR from the University of Alaska's Scenarios Network for Alaskan and Arctic Planning (SNAP, monthly, 1 km resolution), and daily interpolated MODIS average surface temperatures with a linear spline. CCaN pools were initialized with spatially explicit North Slope SOM and Biomass C and N data from Jiang et al. (2016, 2017), and spun-up with 2000–2010 growing season climatology to determine starting values at each site. Decadal average growing season (6/1–8/31) MODIS NDVI was compared to CCaN NDVI, and interannual variability in MODIS NDVI quantified measurement uncertainty at each site.

2.7. Model-Data Fusion

Functional convergence hypothesizes that NEE in all arctic tundra communities responds similarly to temperature, light, LAI, and NDVI throughout time. Hence, CCaN was parameterized using a batch model approach where parameters are estimated simultaneously from data and assumed to be static over space and time.

CCaN was parameterized using a weighted least-squares two-step model-data fusion based on Keenan et al. (2012) and Richardson et al. (2010). The routine was an adaptive Markov-chain Monte Carlo that used Metropolis-Hastings sampling (Metropolis et al., 1953) and incorporated measurement uncertainty into the parameterization, allowing propagation of parameter uncertainty into model predictions. Prior distributions for the seven parameters estimated (Table 1) were assumed to be uniform. The model-data fusion algorithm was corroborated using synthetic NEE and NDVI data from CCaN. Parameters were then estimated using growing season NEE and NDVI data from odd years (i.e. 2009, 2011, 2013, and 2015), leaving data from even years (i.e. 2008, 2010, 2012, 2014) for CCaN corroboration.

To assess goodness of fit of CCaN to NEE and NDVI, we calculated an individual cost function (j_i) as the total uncertainty-weighted squared data-model disagreement for each data type (Richardson et al., 2010) [Eq. (1)].

$$j_i = \left(\sum_{t=1}^{N_i} \left(\frac{y_i(t) - p_i(t)}{\delta_i(t)} \right)^2 \right) \quad (1)$$

Where N_i was the number of observations for data type i , $y_i(t)$ was the data at time t , $p_i(t)$ was the value predicted by the model, and $\delta_i(t)$ was the measurement uncertainty.

In step one, the best parameter set was determined by minimizing the overall cost function (J), which was the product of the individual cost functions (Richardson et al., 2010) [Eq. (2)], treating all data equally by valuing relative improvements in goodness-of-fit (Richardson et al., 2010; Franks et al., 1999).

$$J = \prod_i j_i \quad (2)$$

At each iteration, parameters were randomly drawn from a normal distribution with mean equal to the previous parameter and standard deviation equal to a fraction of the initial parameter range that was adjusted to achieve an acceptance rate of 25–30%, preventing the routine from getting stuck at local minima. Parameters that fell outside of their prior distribution were disregarded and re-drawn. To determine starting values for pools (Table 1), a model-spin up was run for thirty years using decadal averaged daily forcing data. The pool starting values for the model spin-up were determined from previous publications (Jiang et al., 2016). The model was run with the new parameter set and starting values, and the cost functions were calculated. The parameter space was explored in this manner until the overall cost function (J) stopped improving for 20,000 iterations.

In step two, parameter uncertainty was estimated by exploring the parameter space around the parameter set that resulted in the smallest J in step one. Parameters were randomly drawn from a normal distribution with a mean equal to the best parameter and standard deviation held constant at the value from the end of step one. Uncertainty-weighted data-model disagreements were normalized based on the variance of the j_i 's obtained in step one, and parameter sets were only accepted if the cost function for each data stream (j_i) passed a chi-square test at 90% confidence, which ensured that predictions were consistent with each data type (Franks et al., 1999; Richardson et al., 2010; Keenan et al., 2012). Step two was run until 1000 parameter sets were accepted, providing distributions and uncertainty estimates for each parameter.

2.8. Residual Analysis

Daily NEE and NDVI residuals were calculated for the 2008–2015 growing seasons (measured – CCaN). For NEE, negative residuals occurred when CCaN predicted less C uptake than measurements, and positive residuals occurred when CCaN predicted greater C uptake than measurements. For NDVI, negative residuals occurred when CCaN overestimated NDVI, and positive residuals occurred when CCaN underestimated NDVI. Moving averages of these residuals were compared with associated measurement uncertainties of NEE and NDVI and used to assess CCaN prediction biases with time, temperature, PAR, and VPD.

2.9. Sensitivity and Variance Decomposition Analyses

Local and global sensitivity and variance decomposition analyses were conducted for all seven estimated parameters in CCaN (Soetaert and Petzoldt, 2010). The local sensitivity analysis determined model sensitivity based solely on model structure, whereas the global sensitivity analysis estimated 90% confidence intervals for CCaN NEE and NDVI from the quantified parameter uncertainties (i.e. posterior distributions) obtained with model-data fusion.

Local model sensitivity for each parameter (S) was quantified as the average change in model output per change in parameter ($\Delta\text{Output}/\Delta\text{Parameter}$) multiplied by the size of the output and parameter values (Parameter/Output) to treat all parameters equally. CCaN parameters were altered individually and a high average S indicated high sensitivity to model predictions. For the global sensitivity analysis, 90% confidence intervals for CCaN predictions were obtained by simultaneously altering CCaN parameters in accordance with their posterior distributions determined from model-data fusion. Variance decomposition assessed the contribution of parameter uncertainty to CCaN prediction uncertainty. For variance decomposition, each parameter was altered using their associated posterior distribution, while the other model parameters were held constant at their statistical mean. The variance in NEE and NDVI was calculated after variance decomposition was accomplished 1000 times for each parameter. Parameters contributing larger amounts of variance into CCaN predictions signified the most important and dominant processes within the model framework.

3. Results

3.1. Meteorological Data

Weather at the Anaktuvuk site spanned a range of environmental conditions during the measurement period (Table 2). Growing season length ranged from 119 to 139 days with above average growing season lengths in 2008, 2010, and 2012 and below average growing season lengths in 2009 and 2015 (Table 2). 2014 and 2008 were cool and wet growing seasons, whereas 2011 was a cool and dry growing season. 2012 and 2009 were warm and wet growing seasons, whereas 2015 and 2010 were cold and wet growing seasons. Interannual variation in growing season PAR was small with a 0.08 coefficient of variation.

Table 2
Summary of environmental conditions for each growing season.

	2008	2009	2010	2011	2012	2013	2014	2015
Growing Season Length (days)	138	119	136	131	139	128	134	120
Average Temperature (°C)	5.9	7.9	7.9	6.9	7.9	7.1	5.8	7.9
Average PAR (mol m ⁻² day ⁻¹)	31.6	32.4	32.4	35.6	27.6	30.5	27.1	30.8
Total Precipitation (mm)	243.1	271.7	185.9	115	281.9	227.7	276.4	199.6
Average VPD (kPa)	1.8	2.3	1.4	0.9	2.0	1.9	2.1	1.6

Note: The growing season was defined as the time between the date of spring onset and senescence used in the CCaN seasonality scalar (S_{season} ; see appendix).

Growing season VPD was highest in 2009 and lowest in 2011 with a 0.24 coefficient of variation.

3.2. Parameter Estimation and Covariation

The majority of CCaN parameters were uncorrelated, with the exception of litterfall rate (LitterRate) and net N mineralization rate (netNrate), and to a lesser extent LitterRate and the proportion of N in foliage (propN_fol0) (Fig. 3). Model-data fusion improved posterior distributions for all seven parameters with reductions in the 5th and 95th parameter interquartile ranges, and a shift from uniform to approximately normally distributed histograms (data not shown). This constraint of all parameter posteriors illustrated that the NEE and NDVI data were able to adequately inform CCaN parameterization and improve predictions.

3.3. Temporal Corroboration

CCaN captured the magnitudes and seasonal trends in measured NEE and NDVI (Fig. 4A, B). Both CCaN and measured NEE were positive

in the shoulder seasons (i.e. spring and fall) and most negative during peak growing season (Fig. 4A). CCaN and measured NDVI peaked between 0.6 and 0.7, and exhibited similar seasonality with increases in spring and declines in the fall (Fig. 4B).

CCaN NEE explained 17% of the variance in measured NEE for unassimilated years (Fig. 4C), and 77% of NEE measurement and model uncertainties overlapped (Fig. 4A). Overall NEE RMSE was 0.79 with a minimum of 0.52 in 2008 and a maximum of 0.94 in 2013 (Fig. 4E). NEE RMSE decreased when CCaN was assessed at longer time steps (Fig. 5). 8-day, 14-day, and 30-day averaged NEE had an RMSE closer to 0.4, and 90-day averaged NEE had an RMSE of 0.18 (Fig. 5). NEE R^2 increased to ~ 0.6 for 8-day, 14-day, and 30-day time periods, and decreased to 0.06 for 90-day averaged NEE (Table 3).

CCaN NDVI explained 54% of the variance in measured NDVI for unassimilated years (Fig. 4D), and 85% of NDVI measurement and model uncertainties overlapped (Fig. 4B). Overall NDVI RMSE was 0.04 with a minimum of 0.03 in 2008 and a maximum of 0.06 in 2012 (Fig. 4F). NDVI RMSE decreased as CCaN was assessed at longer time-steps, with a minimum of 0.02 occurring for 90-day averaged NDVI (Fig. 5). NDVI R^2 slightly increased to ~ 0.57 for 8-day, 14-day, and 30-

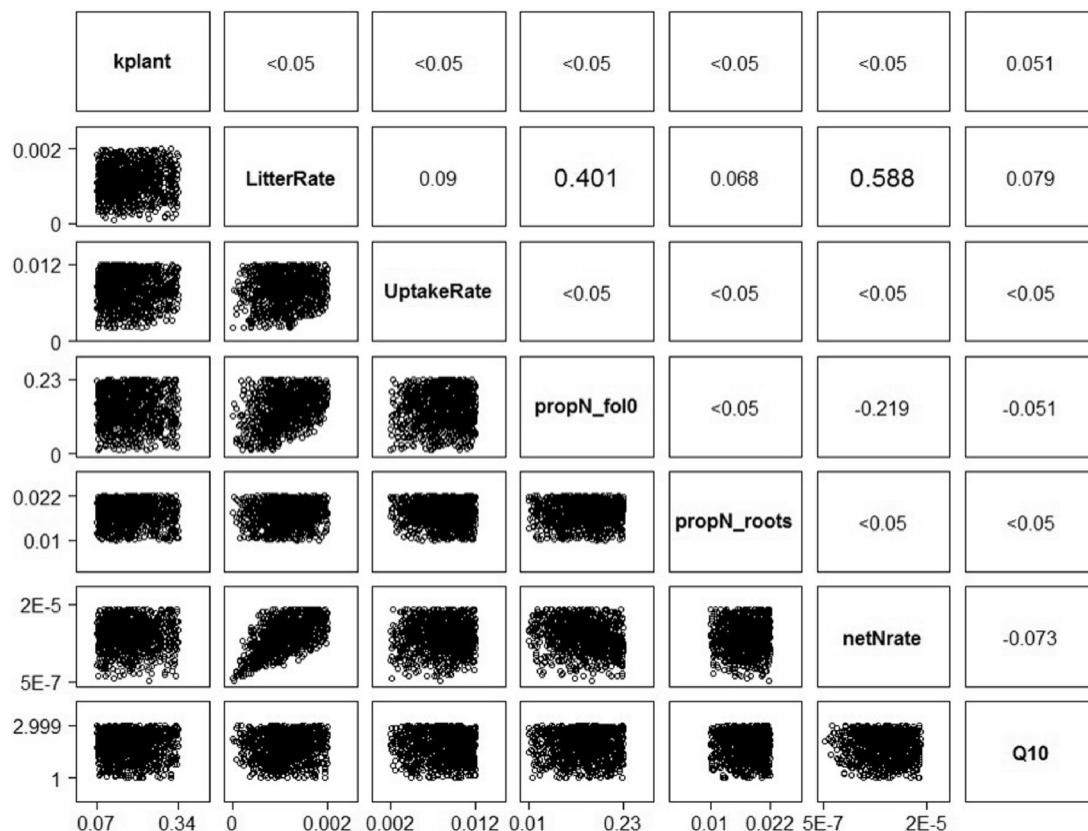


Fig. 3. Parameter correlation plots (left scatter plots) and Pearson correlation values (right numbered boxes) for the seven parameters estimated via data assimilation. Statistically significant correlations at the 90% confidence level are highlighted as bold numbers.

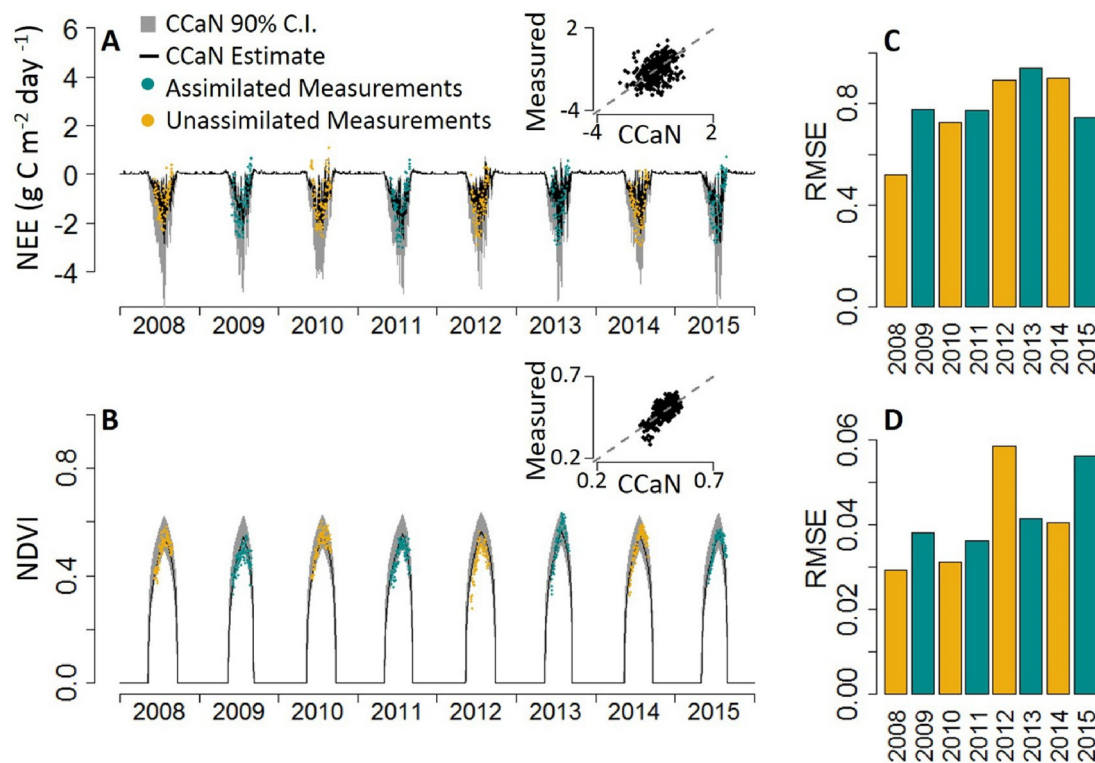


Fig. 4. Comparison of CCaNet NEE and NDVI with observations. Green indicates data that used for parameterization and yellow indicates data used for corroboration. Grey region in A and B indicate 90% confidence interval for CCaNet predictions. A) CCaNet NEE and eddy covariance measured NEE over time and 1:1 comparison of unassimilated years (inset plot). B) CCaNet NDVI and tower measured NDVI over time and 1:1 comparison of unassimilated years (inset plot). C) Yearly NEE RMSE, and D) Yearly NDVI RMSE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

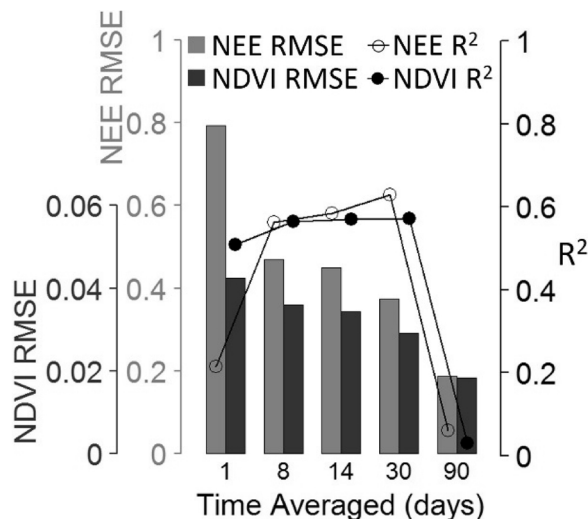


Fig. 5. Changes in CCaNet performance with time. R^2 for 1, 8, 14, 30, and 90 day averaged NEE (open line circles) and NDVI (closed line circles). RMSE for 1, 8, 14, 30, and 90 day averaged NEE (grey bars) and NDVI (dark bars).

day time periods, and decreased to 0.03 for 90-day averaged NDVI.

Seasonal bias in CCaNet NEE occurred in both the spring and fall (Fig. 6A). CCaNet predicted less C uptake than NEE measurements in the spring and residuals fell below measurement uncertainty around day of year 180 (Fig. 6A). CCaNet also predicted greater C uptake than NEE measurements in the fall and residuals fell above measurement uncertainty around day of year 280 (Fig. 6A). NEE biases were unrelated to daily average air temperature with residuals within the measurement uncertainty bounds (Fig. 6B). However, CCaNet NEE biases occurred at low PAR and residuals fell below measurement uncertainty bounds

Table 3

Parameter values and constraint after model-data fusion. Interquartile Range (IQR) is the difference between the 5% and 95% confidence interval of the parameter distribution.

Parameter	Best Value	% of Prior IQR
K_{plant} ($g\ N\ m^{-2}$)	0.1	88.8
LitterRate (Day^{-1})	0.0016	66.3
UptakeRate (Day^{-1})	0.01	73.9
propNfolo ($g\ N\ g^{-1}\ N\ biomass$)	0.13	78.5
propNroots ($g\ N\ g^{-1}\ C\ biomass$)	0.021	84.8
netNrate (Day^{-1})	1.05×10^{-5}	62.4
Q_{10}	2.84	83.6

when daily average PAR was lower than $\sim 20\ mol\ m^{-2}\ day^{-1}$ (Fig. 6C). Average NEE residuals decreased with increasing daily average VPD and fell outside of the measurement uncertainty bounds just above a VPD of $\sim 1.25\ kPa$ (Fig. 6D).

CCaNet NDVI average residuals showed no bias across day of year, daily average air temperature, daily average PAR, or daily average VPD (Fig. 6E–H). Average NDVI residuals fell within measurement uncertainty bounds, and largely remained near zero (Fig. 6E–H). Average NDVI residuals illustrated a slight increase with DOY throughout the growing season, but never fell outside the measurement uncertainty bounds (Fig. 6E).

3.4. Spatial Corroboration

CCaNet NDVI latitudinal trends followed a similar pattern to MODIS NDVI (Fig. 7A). Both CCaNet and MODIS NDVI were highest (~ 0.6) at the low latitude ($< 68^\circ N$) and low-elevation sites ($\sim 69^\circ N$), and lowest at high latitude sites ($> 70^\circ N$) (Fig. 7A). CCaNet and MODIS NDVI were significantly correlated with average growing season temperature, but CCaNet exhibited a slightly lower temperature sensitivity than MODIS

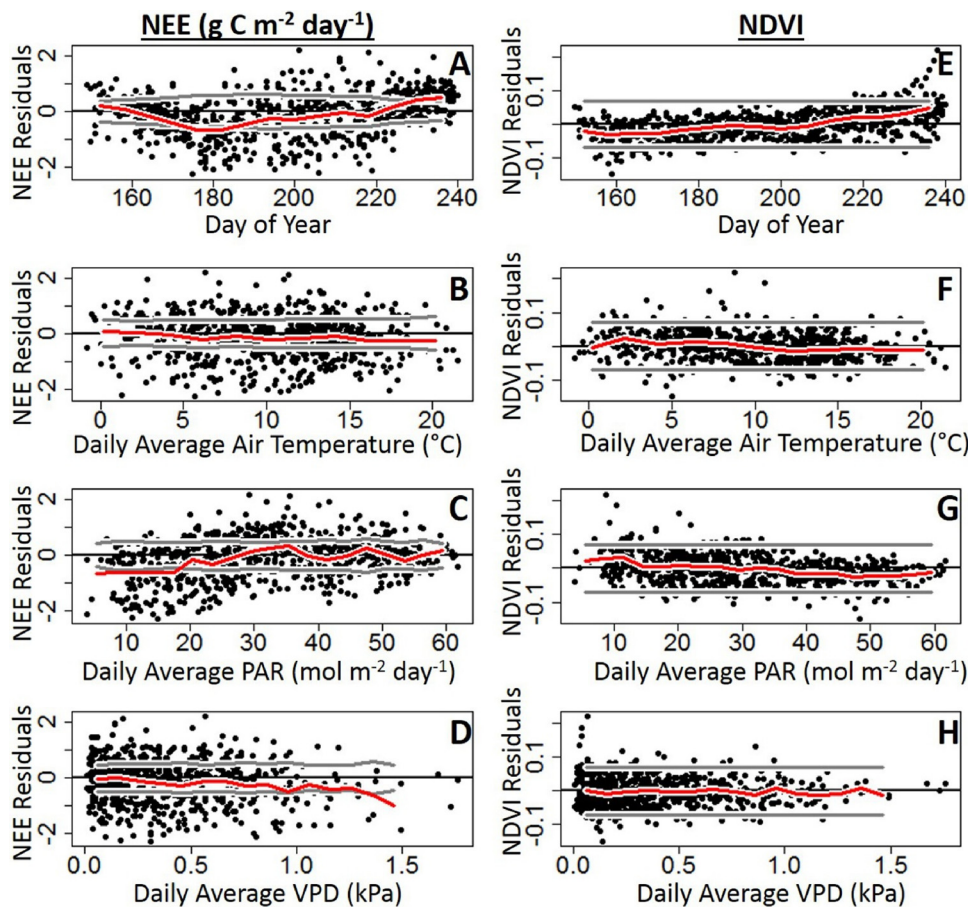


Fig. 6. Residual analysis of NEE and NDVI. For NEE, negative residuals occurred when CCaN predicted less carbon uptake than measurements, and positive residuals occurred when CCaN predicted greater uptake than measurements. For NDVI, negative residuals occurred when CCaN overestimated NDVI, and positive residuals occurred when CCaN underestimated NDVI. The gray lines represent measurement uncertainty and red lines represent average residuals (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

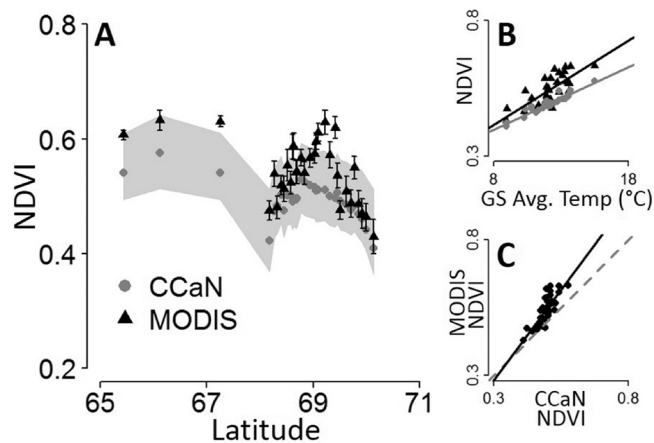


Fig. 7. Spatial corroboration of NDVI in Alaska. A) MODIS NDVI (black triangles) and CCaN (gray dots) NDVI latitudinal variation. Gray shaded area represents modeled 90% confidence interval, while error bars represent MODIS NDVI 90% confidence intervals. B) MODIS (black) and CCaN (gray) NDVI vs. growing season average temperature with lines representing linear regressions, and C) 1:1 comparison of CCaN and MODIS NDVI, with the gray dashed line representing the 1:1 line and the black solid line representing the linear regression.

(Fig. 7B). Consequently, the greatest data-model disagreement occurred at sites with high temperature and high NDVIs (Fig. 7A).

3.5. CCaN Sensitivity and Variance Decomposition

Local sensitivity analysis revealed higher sensitivity of NEE to model parameter changes than NDVI (Fig. 8A). CCaN NEE and NDVI

were most sensitive to changes in litter fall rate (LitterRate), followed by the net N mineralization rate (netNrate), proportion of biomass N in foliage (propNfol₀), and the Q10 of N mineralization (Fig. 8A). CCaN NEE and NDVI were less sensitive to changes in the half saturation of N uptake (K_{plant}), N uptake rate (UptakeRate), and proportion of N in roots (propNroots) than the other four parameters (Fig. 8A).

In contrast with the local sensitivity analyses, variance decomposition revealed that model-data fusion constrained parameter ranges within biologically reasonable values, resulting in different conclusions about CCaN sensitivity (Fig. 8B). The uncertainty in the rate of net N mineralization (netNrate) introduced the greatest amount of annual variance into NEE, followed by the proportion of biomass N in foliage (propNfol₀) and litter-fall rate (LitterRate) (Fig. 8B). NDVI followed the opposite trend, the uncertainty in litter fall rate (LitterRate) introduced the greatest amount of annual variance, followed by the proportion of biomass N in foliage (propNfol₀), and the rate of net N mineralization (netNrate) (Fig. 8B). The uncertainty in the Q10 of N mineralization and the half saturation of N uptake contributed very little to the total annual variance in both NEE and NDVI (Fig. 8B).

4. Discussion

CCaN is a parsimonious model that provided a simple representation of arctic C and N cycling. The model tested several hypotheses that have been put forth about predicting LAI, NDVI, and NEE from coupled C and N cycles (Williams and Rastetter, 1999; Shaver et al., 2013). CCaN was based on the hypothesis of functional convergence that states that arctic NEE can be predicted in both time and space with light, air temperature, and LAI alone using a single response function (i.e. parameter set) (Shaver et al., 2013). We extended the functional convergence hypothesis by including coupled C and N cycling model to

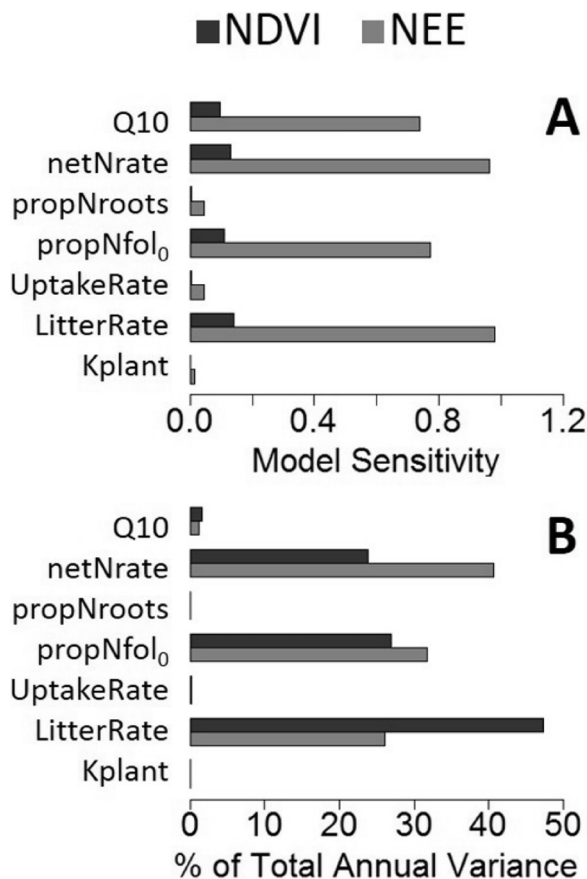


Fig. 8. Sensitivity and variance decomposition analyses for CCaN. A) Model sensitivity to each parameter and B) annual variance contributed by each parameter for CCaN NEE and NDVI.

predict LAI, NDVI, and NEE over time and space. CCaN excluded factors that are important for arctic C and N cycling such as varying response functions for different vegetation types, soil moisture impacts on NEE and N cycling, and the impacts of microbial biomass on C and N cycling within multiple soil layers. However, despite the exclusion of these factors, CCaN performed well in capturing the latitudinal patterns in NDVI and performed similarly to other NEE models (i.e. [Lorant et al., 2011](#); [Jiang et al., 2015](#)). CCaN had higher predictive ability for NDVI than NEE, likely because NEE is a complex flux that involves the response of ecosystem respiration and photosynthesis to environmental factors. Ecosystem respiration and photosynthesis are driven by both rapid changes to the environment and slower changing vegetation and soils. It is clear that increasing the complexity of CCaN's response to the environment would improve its performance. However, an increase in model complexity would stray from the framework of the functional convergence hypothesis model and hinder our ability to diagnose model-data disagreements and highlight important processes and measurements that are needed to improve understanding of arctic C fluxes.

Given the large landscape variability in edaphic, biologic, and climatic factors, it may seem odd that such a parsimonious model could predict arctic ecosystem structure and function across North Slope vegetation communities. However, the strong nitrogen limitation and dependence of C and N cycles on carbon inputs via photosynthesis likely impose strong stoichiometric constraints resulting in functional convergence as an emergent ecosystem property. In arctic ecosystems, nutrients are limited and primarily internally recycled because of high soil organic C and water content, low soil pH, cold temperatures, and low atmospheric deposition ([Shaver et al., 2014](#)). Low soil N availability limits plant productivity, leaf area, soil C inputs, and CO₂ fluxes

because N controls the carboxylation capacity of photosynthesis and biomass/litterfall production ([Heskel et al., 2012](#); [Street et al., 2012](#); [Shaver et al., 2014](#)). The low soil N causes N to be recycled through the system via litterfall resulting in a relatively coupled C and N cycle. These processes as well as the low arctic ecosystem diversity likely create stoichiometric limitations in tundra biogeochemistry that cause functional convergence in C and N cycles, which are driven by the reorganization of C and N among ecosystem pools (i.e. leaves, woody tissue, and soils).

Along with insights into arctic C and N cycles and functional convergence in NEE, our analyses detected statistically significant model-data disagreements that highlight knowledge gaps and areas for future research on arctic NEE. At the daily timescale, CCaN predicted less C uptake at low light levels than indicated by measurements ([Fig. 5C](#)). These observations may be evidence of important mechanisms, such as the enhancement of photosynthesis under low light with high diffuse radiation or the inhibition of leaf respiration at low light [i.e. the Kok effect], which are not included in the CCaN light response function ([Williams et al., 2014](#); [Heskel et al., 2013](#)). At the seasonal timescale, CCaN highlighted a seasonal bias in NEE: predicting lower C uptake in the spring and lower C losses in the fall than indicated by measurements. Higher observed NDVI/LAI could be due to leaf physiological changes, as photosynthesis decline with age ([Bond, 2000](#)). In CCaN, only NDVI/LAI determines maximum photosynthetic rates, as changes in leaf physiology are assumed temporally invariant in accordance with the functional convergence model in [Shaver et al., 2007](#). The seasonal bias is not due to improper representation of LAI, since NDVI/LAI exhibited no such seasonal bias ([Fig. 5E](#)). Changes in the Q10 and basal ecosystem respiration rates is another process that is not included in CCaN that may explain the late season bias in NEE. However, the temperature sensitivity of ecosystem respiration is known to change seasonally from increased thaw depth and soil volume. Although these interpretations are somewhat speculative they are consistent with known ecophysiological process and highlight potential hypotheses that motivate increased understanding of arctic NEE and its seasonal controls.

Our analysis also provided insights into the longer term (i.e. decadal) ecosystem processes that are important for predicting the response of NEE to future climate change. By using a space for time approach with the 7 °C latitudinal temperature gradient, we identified functional differences in C and N cycling responses to the environment between tundra with low and high LAI. CCaN under predicted NDVI in warm tundra ecosystems with LAIs > 1.0 m² m⁻², indicating that these canopies likely deviate from the hypothesis of functional convergence in C and N cycling ([Fig. 6A,C](#)). Because NDVI is directly related to the prediction of NEE through LAI in the functional convergence model, data-model disagreements in NDVI also would carry over into estimates of NEE. In arctic tundra, LAI's above 1.0 are associated with increased vegetation height, canopy complexity, and shrub cover. Shrub tundra differs from graminoid tundra in a variety of ways with greater nutrient use efficiencies, greater ecosystem respiration rates, and greater allocation to woody tissues and leaves ([Williams and Rastetter, 1999](#); [Parker et al., 2015](#); [Koller et al., 2016](#)). The underprediction of NDVI in warm tundra with high LAI in CCaN indicates these systems form a distinct cohort that results in them deviating from the hypothesis of functional convergence in NEE. The implication of this result is that future warming will cause a detectable state shift in ecosystem structure and function that will have consequences for C and N coupling and cycling.

4.1. What measurements are needed to improve CCaN and our understanding of arctic C fluxes?

Understanding the daily and seasonal controls on tundra NEE will require improved measurements of canopy photosynthesis and ecosystem respiration. It is unlikely that NEE alone can provide such

understanding as the long arctic photo-period and measurement limitations challenge partitioning NEE into canopy photosynthesis, and hetero- and auto-trophic respiration. Rather, small-scale leaf photosynthesis and soil respiration measurements throughout the growing season could be used in conjunction with NEE measurements to improve and quantify flux partitioning uncertainties in the arctic. Moreover, proxies of canopy photosynthesis such as the solar induced fluorescence, isotopic (^{13}C , ^{18}O) or other trace gas fluxes (Carbonyl Sulfide (COS)) may further aide in constraining NEE partitioning at the ecosystem scale (Asaf et al., 2013; Baldocchi, 2014; Saleska et al., 2006; Yang et al., 2015). Other measures, such as ecosystem C and N stocks, turnover times and allocation, are likely to be dependent on community composition and may help to disentangle plant versus soil responses to the environment. It is clear from this work that combining multiple measures of ecosystem processes within an analytical framework provides a powerful tool for constraining and further understanding arctic ecosystem function.

Understanding the spatial controls on arctic NEE will require improved knowledge of the biotic and abiotic controls on leaf area and NDVI in tundra ecosystems. Disentangling the ecological mechanisms driving high LAI in tundra ecosystems is critically important as climate change will drive ecosystems into more productive states (Myers-Smith et al., 2011). CCaN suggests that tundra NEE and NDVI are driven more by changes in allocation and turnover rather than biochemical efficiencies associated with plants and microbes (Fig. 7). For example, factors that regulated the efficiency of plant nutrient use (K_{plant}) and microbial temperature responses (Q10) contributed less variance into NEE and NDVI predictions than the factors regulating turnover and allocation of C and N (i.e. LitterRate, propN_{folo}, netNrate, Fig. 7). LitterRate likely explained much of the variability in NDVI because the closed N cycle in CCaN required faster N cycling to support greater LAI. This suggests that warming and shifts in arctic species composition will increase C and N cycling rates among pools (i.e. decrease residence time), and provides motivation for pulse-chase experiments with ^{14}C , ^{13}C , and ^{15}N in high and low LAI tundra canopies (Peterson and Fry, 1987; Carbone et al., 2007). Such experiments will yield insight into the impact of C and N allocation, turnover, and plant nutrient use efficiencies on arctic NEE and NDVI that can be used to constrain these processes in biogeochemical models.

4.2. Conclusions and Implications

We developed a parsimonious model, which included a mass balance of C and N among pools and coupled C and N cycles to predict NEE, LAI, and NDVI. The governing framework of CCaN included the functional convergence model of Shaver et al. (2007) and Shaver et al. (2013) and the tight coupling between leaf N and LAI through a closed coupled C and N cycle. CCaN performed much better in predicting spatial patterns in NDVI and LAI, than predicting temporal variability in NEE. Model sensitivity analyses indicated that the inclusion of field measurements reduced model uncertainty and that better understanding of the factors controlling leaf litter rate, the proportion of N in leaves, and the net N mineralization rate would improve CCaN's predictions.

Our implementation of model-data fusion with CCaN allowed us to diagnose model-data disagreements that were outside of field measurements and model uncertainty, and identify important processes that are missing from such a parsimonious approach. In this case, CCaN served more as a hypothesis on how the system works conceptually, rather than serving solely as a predictive tool. Understanding where and when a model fails can result in further mechanistic understanding and highlight significant knowledge gaps provided that the uncertainty in the measurements and models are properly quantified. Moreover, our approach also allowed us to incorporate diverse datasets, such as from the Arctic LTER, to help inform biologically realistic parameter values. Such an approach could be used elsewhere, and it is clear that using

model–data fusion for model parameterization is ideal for gaining a greater understanding of ecological systems through modeling.

There have been, and will continue to be, changes in species composition and canopy structure as northern latitudes warm (Goetz et al., 2005; Myers-Smith et al., 2011). Many of these changes are happening at rates faster than we can measure them. Hence, developing models that can forecast these changes remains a high priority for justifying measurement campaigns in global change biology research. This study highlights a further need to understand the biotic and abiotic factors controlling the component fluxes of NEE (i.e. photosynthesis, auto-trophic, and heterotrophic respiration) as well as C and N cycling in warm tundra ecosystems with high leaf area. Our model-data comparison also emphasized a need to understand how temperature influences plant C allocation, and ecosystem C and N turnover in tundra with high LAI and warm climates. This is important because C and N fluxes and cycling in these systems is poorly understood; a search on Ameriflux reveals an underrepresentation of arctic NEE measurements from warm shrub tundra sites. Further validation of CCaN in shrub tundra would be needed to determine the reason the model performed poorly in these systems. Improved understanding of such systems will determine whether the vegetation response to climate change will offset C losses from thawing permafrost (Stieglitz et al., 2006; Hicks Pries et al., 2013; Schuur et al., 2015; Abbott et al., 2016).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2018.05.017>.

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